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AN INQUILINE SPECIES OF *TAMALIA* CO-OCCURRING WITH *TAMALIA COWENI* (HOMOPTERA: APHIDIDAE)

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Abstract.—*Tamalia inquilinus* Miller, NEW SPECIES, is described from California and is compared with its frequent gall-inducing associate, *Tamalia coweni* (Cockerell). A key is presented for distinguishing the known species of *Tamalia.* It is suggested that *T. inquilinus* may be entirely dependent on *T. coweni* for the induction of galls that the two species co-occupy.

Key Words.—Insecta, aphid, gall, inquiline, *Tamalia, Arctostaphylos.*

The genus *Tamalia* Baker 1920 comprises five described species, distributed primarily in western North America. All are distinguished by winged oviparae, greatly reduced siphunculi, and all occupy galls on *Arctostaphylos* spp. (Ericaceae), with the exception of some populations causing galls on the closely related *Arbutus arizonica* and which may represent an undescribed species (Miller, unpublished data). Here we describe a novel species, *Tamalia inquilinus* Miller, an inquiline of *Tamalia coweni* (Cockerell 1905). We present data suggesting that *T. inquilinus* is at least facultatively or possibly obligately associated with *T. coweni* in galls on several *Arctostaphylos* spp. We provide tables, based on the most distinctive morphological characters, for distinguishing the two species. A key is presented for separating all five species of *Tamalia,* modified from those of Richards (1967) and Remaudière & Stroyan (1984). We follow the classification scheme of Remaudière & Stroyan (1984) and Nieto Nafría et al. (1997), placing *T. inquilinus* in the subfamily Tamaliinae Oestlund 1922. DGM is the sole author of the description of *T. inquilinus*.

KEY TO THE SPECIES OF *TAMALIA* BAKER

1. Aptera with 5 or 6 antennal segments, ultimate rostral segment (URS) 160–190 μm, body color probably black (in life), sclerotization of terga complete, second segment of hind tarsus (HT2) 82–104 μm. Alate morphs: URS 210 μm, HT2 130 μm .... *dicksoni* Remaudière & Stroyan
   Aptera with 5 or fewer antennal segments, URS < 110 μm, body color variable, sclerotization of terga variable, HT2 < 85 μm. Alate morphs: URS < 180 μm, HT2 < 130 μm 2
2. Aptera with 5 antennal segments, body color dark grey to brown to black, sclerotization complete, HT2 63–85 μm. Alate morphs: URS 63–83 μm, HT2 50–88 μm .... *inquilinus,* NEW SPECIES
   Aptera with 4 antennal segments, body without pigment or brown, not black; sclerotization incomplete, HT2 ≥ 75 μm. Alate morphs: URS 100–175 μm, HT2 ≥ 75 μm 3

3. Aptera without pigment, sclerotization none, maximum length of head setae: basal diameter of antennal segment III (HS : BANT3) = 1. Alate morphs: HT2 75 μm, without pigment on abdomen and appendages ... . *pallida* Richards*
   Aptera with color, sclerotization partial, HS : BANT3 > 1. Alate morphs: HT2 > 75 μm, abdomen and appendages pigmented 4
4. Aptera with sclerotization in bands, HS : BANT3 = 1.5. Alate morphs: URS 100 μm, HT2 125 μm .... *coweni* (Cockerell)
   Aptera with sclerotization in spots, HS : BANT3 = 2.2. Alate forms: URS 175 μm, HT2 125 μm .... *keltoni* Richards

*because *T. pallida* is distinguished from other *Tamalia* essentially by its lack of pigment, some authors (e.g., Remaudière & Stroyan (1984)) question the validity of *T. pallida.*

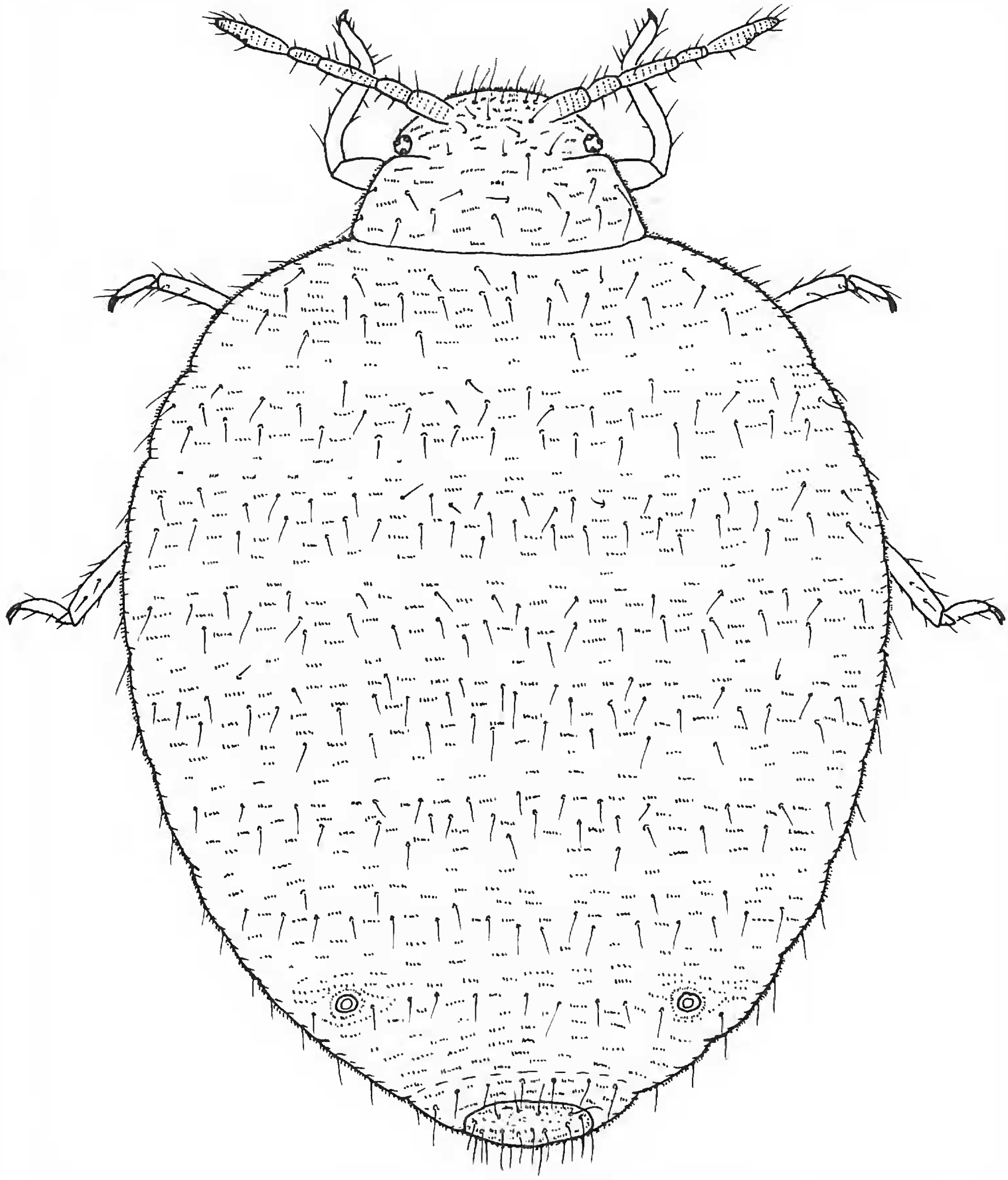
Tamalia inquilinus Miller, New Species

Dimensions given as means, with range in parentheses. All measurements in μm unless indicated otherwise. Wingless gall-inhabiting individuals collected from the first galls of the spring generation may represent the fundatrix generation but, based on twenty-nine morphological characters, these are indistinguishable from later-season apterae. Further, Palmer (1952) and Richards (1967) fail to distinguish between the fundatrix and later generations of apterae, as pointed out by Remaudière & Stroyan (1984) and Miller (1998). Therefore, we refer to all wingless females as apterous viviparae.

Diagnosis.—The adult apterous vivipara of *T. inquilinus* is recognized by the short apical rostral segment, presence of five antennal segments, abundant body setae, and complete sclerotization. Sexuals of *T. inquilinus* are distinct in the relatively short dimensions of the ultimate rostral segment, second segment of the hind tarsus, hind tibia, and antennal segments III and V. These characters serve to separate *T. inquilinus* from all other species of *Tamalia.*

Description.—Apterous vivipara, first-instar (n = 5 specimens): color in life pallid, almost without pigment. Little or no sclerotization present. In life, antenna directed anteriorly in front of body. Setae on terga tapered, not capitate; setae sparsely distributed over surface of cuticle. Body length (BL) (mm) 0.556 (0.495–0.605). Length of hind femorotrochanter (HFEM) 104 (85–128). HFEM width 36.8 (28.8–45.0). Length of second segment of hind tarsus (HT2) 43 (36–53). Maximum length of setae on tergum III (ST3) 24.3 (13.8–33.8). Maximum length of caudal setae 26.3 (21.3–37.5). Length, antennal segment I (ANT1) 26 (23–28); ANT2 26.8 (25.0–32.5); ANT3 54.8 (40.0–71.3); base of ANT4 (LB) 43 (33–53); processus terminalis of ANT4 (LPT) 19 (16–23). Total antennal length (ANT) 168.3 (138.8–206.3). Rostrum extending as far as coxa III. Rostrum (mm): 0.176 (0.135–0.215); ultimate segment of rostrum (URS) 46 (38–58). Number of secondary rhinaria: (3–5). Basal diameter ANT3 (BANT3): 15.5 (11.3–23.8). Min. distance between triommatidia and vertex 86 (75–108). URS : BL 0.083 (0.066–0.105). ST3 : BANT3 1.6 (1.2–3.0). LPT : LB 0.44 (0.41–0.50). ANT3 : ANT2 2.03 (1.60–2.57). ANT : BANT3 11.41 (8.11–13.33). URS : HT2 1.07 (0.97–1.16).

Apterous Vivipara, Adult (n = 12) (Fig. 1)—color in life variable, generally dark grey to brown to black; head often paler than abdomen. Dorsum of body completely and heavily sclerotized, densely covered with setae and spicules. Eye limited to triommatidion. Siphunculus very short, almost poriform. Antenna usually five- (sometimes six-) segmented (Fig. 2). Antennal segment V often darker than segs. I–IV; unguis not sharply defined in segment V. BL (mm) 1.53 (1.37–1.71). Hind tibia (mm) 0.26 (0.22–0.36). HT2 74 (63–85). Number of setae on tarsus I (2–4). ST3 101 (90–110). Maximum length of caudal setae 94 (80–103). Minimum length of caudal setae 41 (30–58). Maximum length of head setae (HS) 77 (65–95). ANT1 55 (45–70); ANT2 53 (45–63); ANT3 109 (75–148); ANT4



Figures 1–2. Adult aptera of *Tamalia inquilinus*. Figure 1. Dorsal view.

55 (35–78); base of ANT5 (LB) 81 (69–96); processus terminalis of ANT5 (LPT) 36 (24–55). ANT 389 (326–494). Maximum length of setae, ANT3 36 (33–44). Rostrum (mm) 0.28 (0.23–0.31); URS 85 (63–105). Rostrum extending as far as just past coxa II. Secondary setae on URS (6–8). URS : HT2 1.16 (0.96–1.48). Number of secondary rhinaria (2–5). BANT3 19 (16–24). Max. : min. length caudal setae 2.40 (1.57–3.42). ST3/BANT3 5.27 (4.11–6.29). HS : BANT3 4.01 (2.84–5.07). LPT : LB 0.45 (0.30–0.66). Max. length setae ANT3 : BANT3 1.87 (1.42–2.33). ANT3 : ANT2 2.06 (1.50–2.53). ANT : BANT3 20.12 (17.67–24.15).

Larva ex Aptera (n = 5)—color in life pallid; body with little or no sclerotization. Setae on terga tapered. BL (mm) 0.63 (0.57–0.73). HFEM 133 (120–148). HFEM width 46 (40–51). HT2 58 (51–70). ST3 44 (38–53). Maximum length of caudal setae 47 (40–51). ANT1 38 (35–43); ANT2 35 (31–41); ANT3 73 (64–81); base, ANT4 (LB) 56 (53–65); processus terminalis of ANT4 (LPT) 24 (20–29). ANT 226 (205–246). Rostrum (mm) 0.24 (0.23–0.26); URS 58 (55–63). Rostrum extending as

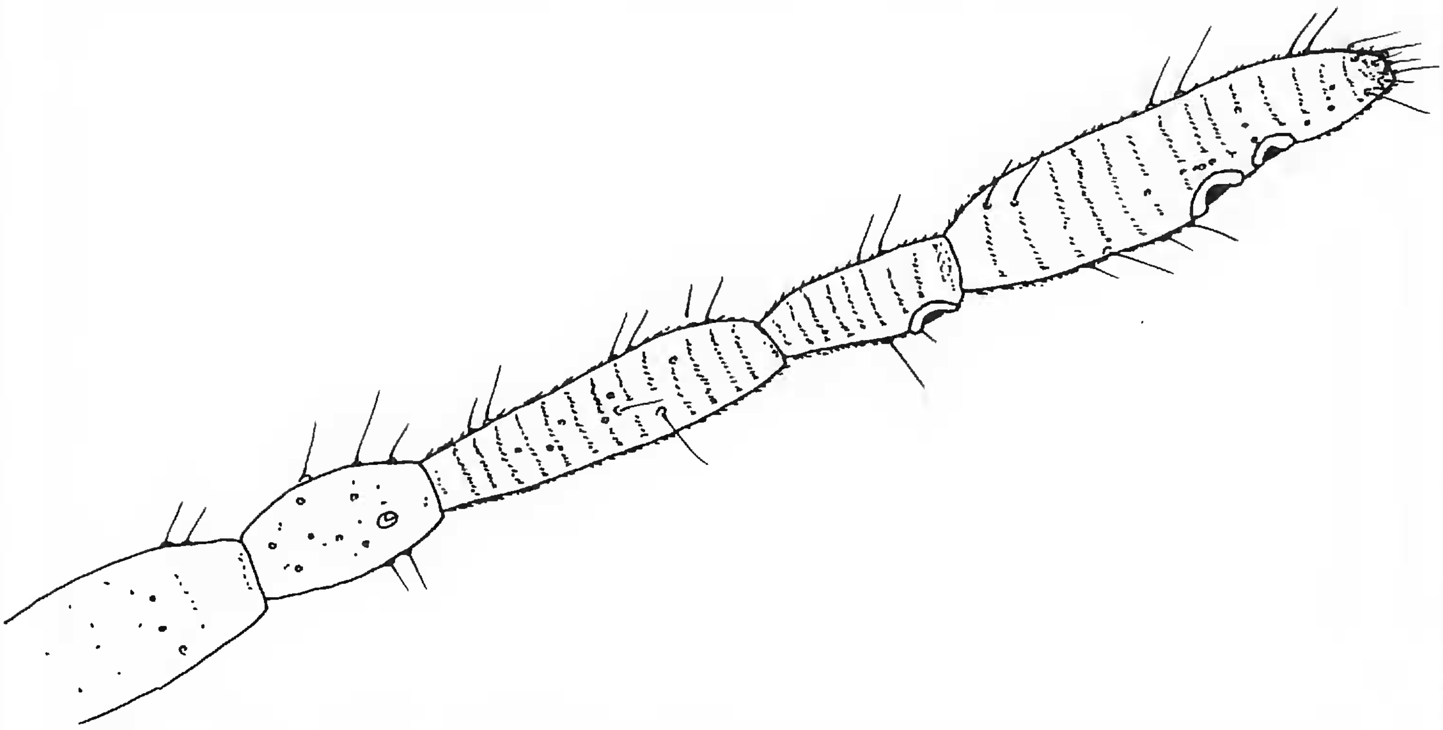
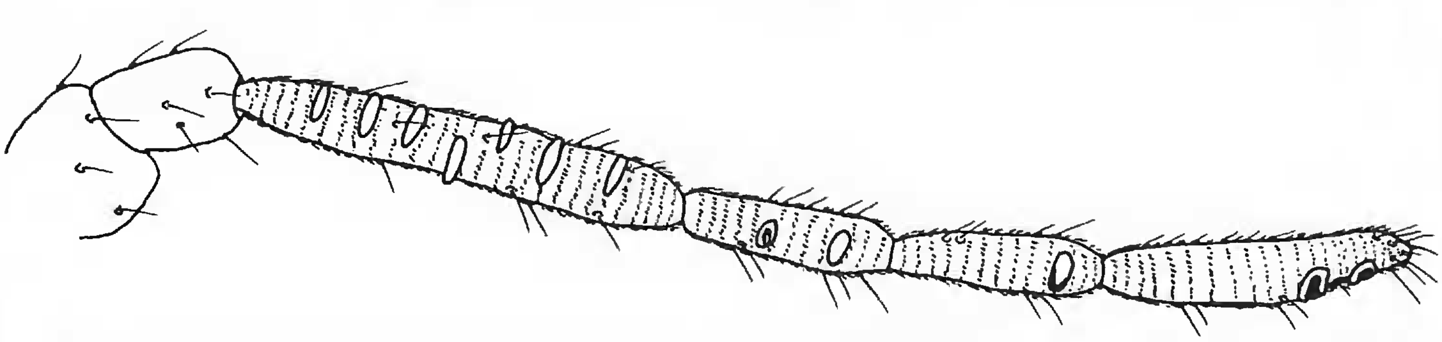


Figure 2. Right antenna, dorsal view.

far as just past coxa III. URS : HT2 0.99 (0.89–1.07). Number of secondary rhinaria 3–5. BANT3 17 (15–23). Min. distance between triommatidion and vertex 132 (113–145). URS : BL 0.09 (0.08–0.10). ST3 : BANT3 2.60 (2.14–3.08). LPT : LB 0.43 (0.38–0.44). ANT3 : ANT2 2.10 (1.94–2.32). ANT : BANT3 13.48 (10.94–15.25).

Ovipara, Adult (n = 5)—Color in life pale green. Wings and compound eyes well-developed; pleura V–VII with cribriform plates which are often covered with waxy secretions. Siphunculus very short. BL (mm) 1.41 (1.22–1.66). Hind tibia (mm) 0.40 (0.36–0.44). HT2 71 (50–80). Number of setae on tarsus I (2–4). ST3 46 (40–55). Maximum length of caudal setae 83 (75–90). Minimum length of caudal setae 14 (13–15). HS 12 (11–13). ANT1 60 (55–68); ANT2 48 (45–53); ANT3 188 (178–198); ANT4 99 (88–113); ANT5 94 (83–108); base of ANT6 (LB) 94 (88–100); processus terminalis of ANT6 (LPT) 41 (38–45) (Fig. 3). ANT 623 (585–675). Maximum length of setae, ANT3 14 (14–15). Rostrum (mm) 0.23 (0.18–0.28); URS 70 (63–73) (Fig. 4). Rostrum extending halfway between coxae I, II. Secondary setae on URS (5–8). URS : HT2 1.02 (0.89–1.45). Number of secondary rhinaria (2–4). BANT3 12 (11–13). Number of secondary sensoria on ANT3 9 (7–10). Max. : min. length caudal setae 6 (5–7). ST3 : BANT3 3.8 (3.2–4.4). HS : BANT3 1.02 (1.00–1.11). LPT : LB 0.44 (0.41–0.49). Max. length setae ANT3 : BANT3 1.19 (1.10–1.33). ANT3 : ANT2 3.92 (3.71–4.16). ANT : BANT3 51.9 (46.8–54.0).

Male, Adult (n = 5)—color in life bright green. Wings and compound eye well-developed; siphunculus very short. BL (mm) 0.98 (0.86–1.10). Hind tibia (mm) 0.43 (0.33–0.50) (Fig. 5). HT2 80 (70–88). Number of setae on tarsus I (4–6). ST3 28 (23–30). Maximum length of caudal setae 47 (40–58). Minimum length of caudal setae 16 (13–18). HS 12 (9–14). ANT1 60 (48–65); ANT2 49 (48–50); ANT3 214 (198–235); ANT4 118 (100–140); ANT5 112 (100–123); base of ANT6 (LB) 99 (90–105); processus terminalis of ANT6 (LPT) 45 (43–48) (Fig. 6). ANT 696 (633–758). Maximum length of setae, ANT3 17 (14–19). Rostrum (mm) 0.24 (0.20–0.29); URS 77 (70–83). Rostrum reaches coxae II. Secondary setae on URS (6–8). URS : HT2 0.97 (0.80–1.14). Number of secondary rhinaria (2–



Figures 3–6. Adult sexuals of *Tamalia inquilinus*. Figure 3. Right antenna of ovipara, dorsal view.

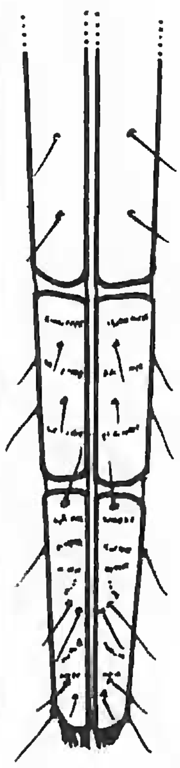


Figure 4. Terminal segments of rostrum of ovipara, ventral view.

4). BANT3 12 (11–14). Number of secondary sensoria on ANT3 3 (2–4). Max.: min. length caudal setae 3.1 (2.3–4.6). ST3 : BANT3 2.3 (2.0–2.7). HS : BANT3 0.97 (0.64–1.11). LPT : LB 0.45 (0.43–0.47). Max. length setae ANT3 : BANT3 1.36 (1.00–1.56). ANT3 : ANT2 4.37 (3.95–4.70). ANT : BANT3 57.3 (50.5–67.3).

Material Examined.—The following is a summary of collection data for galls containing either *T. inquilinus, T. coweni,* or both species. U.S.A., CALIFORNIA, *El Dorado Co.:* Blodgett Forest Research Station, 1350 m, Jul, Aug 1993–1995, on *Arctostaphylos patula* and *Arctostaphylos viscida*; Georgetown, 800 m, Jun–Jul 1995, on *A. viscida*; Lotus, 200 m, Jun 1995, on *A. viscida*; *Placer Co.:* Sagehen Creek Research Station, 1900 m, Aug 1995, on *A. patula*; *Stanislaus Co.:* Kennedy Creek, 2200 m, Jul 1997, on *A. patula*; *Tuolumne Co.:* Sugar Pine, 1300 m, Jul 1997, on *Arctostaphylos mariposa*; *Napa Co.:* Mt. St. Helena, 900 m, Aug 1997, on *Arctostaphylos* spp.; *San Bernardino Co.:* San Bernardino Mts, Mill Creek Canyon, 1000 m, May 1998, on *Arctostaphylos glauca*; *Placer Co.:* junction of North and Middle Forks of American River, 250 m, Jun 1998, on *A. viscida*; *Riverside Co.:* Deep Canyon, 1200 m, Jul 1998, on *A. glauca*; Santa Rosa Mts, 2200 m, Jul 1998, on *A. patula*, and at 1400 m on *A. glauca*; *San Diego Co.:* San Felipe, 1100 m, Jul 1998, on *A. glauca*. MEXICO, Baja California Norte, Sierra San Pedro Mártir, 1250 m, Apr 1998, on *A. glauca*; Interior Coast Ranges, km 32, hwy 3, 300 m, Apr 1998, on *A. glauca*. Specimens were preserved in 95% EtOH, then macerated in 5% KOH, cleared in 30% lactic acid and mounted on slides in a phenol-lactic acid-polyvinyl alcohol medium (BioQuip). All material collected by D. G. Miller.

Type Material.—Holotype: apterous vivipara. U.S.A., CALIFORNIA, *Riverside Co.:* Santa Rosa Mt, 1200 m, 10 Jul 1998, on *A. glauca*. Collection no. S98040b. (The holotype is on the upper right hand side of a slide mounted with four other apterous viviparae.) Morphotypes: ovipara, *Riverside Co.:* Santa Rosa Mt, 1400 m, 26 Jul 1998, on *A. glauca* (specimen is in the center of a slide mounted with one other ovipara and three males), collection no. S98025c; male, *Riverside Co.:* Santa Rosa Mt, 2200 m, 26 Jul 1998, on *A. patula* (specimen is on the lower left hand side of a slide mounted with two other males and two oviparae), collection no. S98029d. Holotype and morphotypes deposited NMNH. Paratypes: *Stanislaus Co.:* Kennedy Creek, 2200 m, 27 Jul 1997, on *A. patula,* 1 aptera; *Tuolumne Co.:* Sugar Pine, 1300 m, 27 Jul 1997, on *A. mariposa,* 2 apterae; *El Dorado Co.:* Blodgett Forest, 1350 m, 28 Jul 1994, on *A. patula,* 1 aptera; Blodgett Forest, 1350 m, 17 Jul 1997, on *A. viscida,* 4 apterae; *Napa Co.:* Mt. St. Helena, 1000 m, 2 Aug 1997, on *Arctostaphylos* spp., 2 apterae; *Riverside Co.:* Santa Rosa Mt, 1400 m, 26 Jul 1998, on *A. glauca,* 2 oviparae, 2 males; *San Bernardino Co.:* Mill Creek Canyon, 1000 m, 24 Jul 1998, on *A. glauca,* 2 oviparae, 2 males. Paratypes deposited at the following museums: Essig Museum, University of California at Berkeley; University of Kentucky Entomological Collection; Trinity University Invertebrate Collection, San Antonio, Texas. All specimens collected by D. G. Miller.

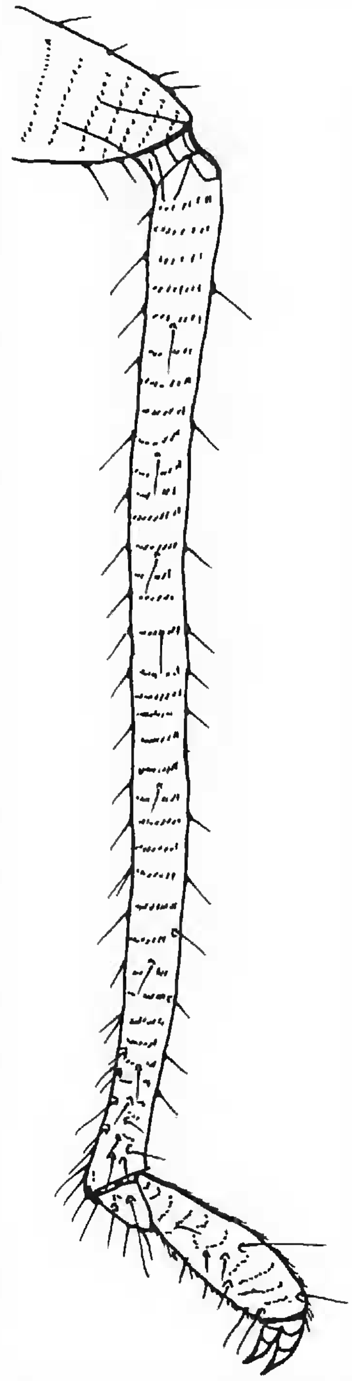


Figure 5. Tibia and tarsus of metathoracic leg of male, dorsal view.

Occurrence of T. inquilinus with T. coweni.—The type series is based on 1739 galls on *Arctostaphylos* spp. that were collected between 1993–1998: as determined by the identification of apterae, 1506 contained *T. coweni* only, 155 both *T. coweni* and *T. inquilinus,* and 78 *T. inquilinus* only. Of the sampled galls containing *T. inquilinus,* over 66% contained *T. coweni* as well; thus, the life history of *T. inquilinus* appears closely associated with that of its congener. All galls collected were typical for those of *T. coweni* regardless of the occupants: galls containing solely *T. inquilinus* are indistinguishable externally from those with *T. coweni* or with both species present. *Tamalia* galls are typically formed by apterae causing the *Arctostaphylos* leaf to roll and swell, thus enclosing the occupants; this type of gall was collected on leaves of *A. patula, A. viscida* and *A. glauca.* Additionally, *T. coweni* can cause galls on inflorescences of *A. patula*; this gall type is termed a flower bud gall (Miller 1998) and was part of the sample as well.

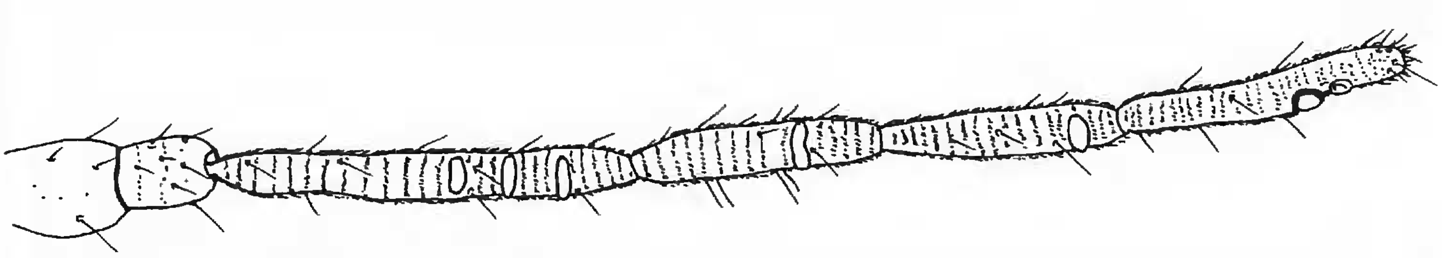


Figure 6. Right antenna of male, dorsal view.

Discussion

Based on its biology and morphology, *T. inquilinus* is considered distinct from *T. coweni* and thus constitutes a novel species. Tables 1 and 2 provide morphological comparisons of *T. inquilinus* and *T. coweni.* For separating *T. inquilinus* from the three other described members of the genus, *Tamalia pallida* Richards 1967, *Tamalia keltoni* Richards 1967, and *Tamalia dicksoni* Remaudière & Stroyan 1984, we refer to the above key and to descriptions given by Richards (1967) and Remaudière & Stroyan (1984). *Tamalia pallida* is recognizable by the absence or reduction of pigment in live and preserved specimens. In *T. keltoni,* the fundatrix, alate vivipara and ovipara bear pigmented spots, unlike other members of the genus. All known morphs of *T. dicksoni* are characterized by the extraordinary length of the apical segment of the rostrum.

Because *T. inquilinus* is so closely associated with *T. coweni,* it occurred to us that *T. inquilinus* is but a morph of *T. coweni,* representing an alternative life history pathway of *T. coweni.* This was the original hypothesis stated in Miller (1998), who referred to apterae of *T. inquilinus* as accessory wingless females of *T. coweni.* However, in all stages of the life cycle here examined, including aptera, larvae ex aptera, ovipara and male, morphological features occur which allow reliable separation of the two species concerned.

Although *T. coweni* is widely distributed in North America, ranging from Ontario across boreal Canada and much of western North America south to Mexico (Richards 1967, Remaudière & Stroyan 1984), *T. inquilinus* is reported only from Northern California south on the Pacific Slope to Baja California Norte, Mexico. That two-thirds of the *T. inquilinus* sampled co-occurred in galls with *T. coweni* indicates *T. inquilinus* may be an obligate inquiline of *T. coweni.* All described species of *Tamalia* develop in galls on *Arctostaphylos: T. inquilinus* appears to be no exception. The galls containing *T. inquilinus* but without *T. coweni* may have been founded by *T. coweni* apterae before the arrival of *T. inquilinus* apterae; thereafter, the founding *T. coweni* may have exited the gall. This is possible as all generations of apterae of *T. coweni* are capable of founding galls (Miller 1998) and foundresses of *T. coweni* often abandon galls (Miller, unpublished data). However, more data are needed to test the hypothesis that *T. inquilinus* has lost the ability to cause galls and is obligately associated with *T. coweni.*

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Table 1. Comparison of asexual morphs of *T. inquilinus* with *T. coweni*. Metrical data given as range.

	Aptera (adult)		Aptera (first instar)		Larva ex aptera	
	T. inquilinus	*T. coweni*	*T. inquilinus*	*T. coweni*	*T. inquilinus*	*T. coweni*
Body color in life	grey to brown to black	dark olive-brown	white	pale-dark green	white	pale green
Degree of sclerotization	complete	partial	little/none	much	little/none	partial
Shape of setae on tergites	tapered	tapered	tapered	capitate	tapered	tapered
Length of femorotrochanter III (μm)	nr[a]	nr	85–128	130–145	120–148	120–145
Length of rostrum (mm)	0.23–0.31	0.22–0.30	0.14–0.22	0.12–0.20	0.23–0.26	0.18–0.20
Color of antennae	ant. seg.V often darkest	uniform	uniform	uniform	uniform	uniform
Shape of unguis	not sharply defined	sharply defined	nr	nr	nr	nr
Antennal segment II (μm)	45–63	35–45	25–33	26–29	31–41	29–31
Basal length, segment IV (μm)	not present	44–64	33–53	36–49	53–65	45–54
Basal length, segment V (μm)	69–96	np[b]	np	np	np	np
Max. length caudal setae (μm)	80–103	43–78	21.3–37.5	25.0–43.8	40–51	40–44
Length of setae tergite III : diameter ant. seg. III	4.11–6.29	2.67–4.00	1.2–3.0	1.2–2.3	2.14–3.08	1.14–1.55
Total ant. length : diameter, ant. seg. III	17.67–24.15	12.06–16.35	8.11–13.33	9.57–14.00	10.94–15.25	8.24–8.88

[a] Not recorded.
[b] Not present.

Table 2. Comparison of sexuals of *T. inquilinus* with *T. coweni*. Metrical data given as range.

	Ovipara		Male	
	T. inquilinus	*T. coweni*	*T. inquilinus*	*T. coweni*
Body color in life	pale green	rich green	bright green	pale green
Body length (mm)	1.22–1.66	1.50–1.75	0.86–1.10	1.24–1.72
Length of tibia III (mm)	0.36–0.44	0.43–0.57	0.33–0.50	0.61–0.73
Seg. II, hind tarsus (HT2) (μm)	50–80	73–93	70–88	108–128
Ultimate seg. of rostrum (URS) (μm)	63–73	95–108	70–83	80–90
Min. length caudal setae (μm)	13–15	13–20	13–18	18–25
Antennal segment III (μm)	178–198	225–250	198–235	260–345
Antennal segment V (μm)	83–108	110–130	100–123	135–210
Total ant. length (μm)	585–675	685–755	633–758	785–1120
Ant. seg. III/II	3.71–4.16	4.52–6.00	3.95–4.70	4.95–5.96
Length of processus terminalis/base, ant. seg. VI	0.41–0.49	0.26–0.37	0.43–0.47	0.36–0.43
# secondary sensoria, ant. seg. III	8–10	9–16	2–4	4–7
# secondary rhinaria, ant. seg. VI	2–4	5–8	2–4	4–6
URS/HT2	0.89–1.45	1.09–1.41	0.80–1.14	0.67–0.79

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